

also in the extensive district of North America, where no more than a few insignificant species are known to exist. It is in the richly fertile and woody district of Columbia that the genus *Bulimus* is represented with a magnificence little inferior to that of the Philippine Islands : here they are large enough and sufficiently abundant to be roasted and eaten by the aborigines, as a frequent article of food. Several fine species, entirely new to science, have been collected in Venezuela and New Granada by Mr. Linden, an assiduous botanical traveller, only within the last twelvemonth, at an altitude of 5000 to 8000 feet, and many more, no doubt, dwell in undisturbed solitude in the vast interior of that immense continent. It is extremely probable that a large portion of South America yet remains to be explored by the adventurous naturalist, inclosing a fine expanse of forest country, grand in extent, rich in foliage, and possessing all the elements favourable to the growth and beauty of arboreal mol-lusks.

XXVIII.—*Reports on the Progress of Physiological Botany.*

No. 3. By ARTHUR HENFREY, F.L.S. &c.

On the Growth of Leaves.

IN that remarkable book, Hales's 'Vegetable Staticks,' we find the account of an experiment made to determine the mode of growth and expansion of leaves. The method Hales adopted was to *tattoo*, as it may be called, young leaves with punctures made by means of a little instrument on which pins were fixed at determinate distances in parallel rows. In the fig-leaves on which he experimented he found that the punctures were separated from one another during the growth, but maintained their relative distances unaltered, and from this he concluded that "the growth and expansion were owing to the dilatation of the vesicles in every part." In his figures, however, it may be noticed that the leaf has grown more at the *borders and apex* than within the punctures.

Similar experiments have recently been made by M. Gaudichaud*, and he makes the following meagre statements in regard to the petioles and leaves. (The marks were made on young plants of the horse-chestnut raised from seed.) The marks made on the petioles increased their distance two or three times the diameters, equal or unequal, of the original measures, and the proportions of the upper parts generally exceeded those of the lower. It might be imagined that the blades of the leaves would be

* Comptes Rendus, May 10th, 1847.

subject to the same law of growth, but they present more anomalies than any other parts. He states that these are however more apparent than real, and promises to give a detailed account at some future time.

The generally received opinion with regard to the growth of leaves is that, in contrast to the stem, they grow at their base only, and their summits are therefore considered to be the oldest parts.

Link* however states that the leaf appears at once in the bud with all its parts formed, and that it then grows by interstitial development, but mentions one exception, in the Walnut, where the leaves appear ternate or tripartite at first, and the other lobes appear subsequently. Schleiden† declares that the apex is the oldest part and the base the youngest, and that although the process of development within the leaf may increase its size and influence its internal structure, it has no power of determining its form; while to complicate the subject still more, Nägeli ‡ has just published a paper advocating the diametrically opposite opinion. His views are so definitely expressed that they well merit an examination.

In the first place he draws a marked distinction between two modes of growth which necessarily exist in all leaves, viz. 1. *growth by cell-formation*, and 2. *growth by the expansion of the cells*. Considering the fronds of the Algæ to represent leaves, he first points out how these grow by their apices and borders, the increase in length resulting from the continual division of the *apical cell (scheitel-zelle)*, and the increase in breadth, where the lobe or branch consists of several parallel rows, by the development of the outer marginal cells. The same occurs in the *Characeæ*. In the *Hepaticæ*, if the leaf consists of a branched series of cells (as in *J. tricophylla* and *J. setacea*), it grows by the apical cells as in the *Florideæ*. If the leaf is a layer of cells—in the Mosses it possesses *one* continually developing apical cell and the lateral growth is simultaneously effected by the division of the cells left behind as it were by the apical cell, which divide by a septum at right angles to that of the primary cell, and the first two producing four, the outer one of each pair repeats the process, and so on till the whole growth in width is completed. In the *Hepaticæ* when the leaves are layers or plates of cellular tissue like those of the Mosses just described, the process is similar, except that they appear generally to have several *apical* or *primary* cells. When the leaves are more than one layer thick, as is often the case in the midnerve, septa are found in the cen-

* Elem. Philosophiæ Botan. i. 438.

† Grundz. der Wiss. Botanik, 2nd edit. vol. ii. p. 172.

‡ Schl. and Nägeli's Zeitschr. für Wiss. Bot. part 3, 153.

tral cells parallel with the surface of the leaf, and the process extends outward from the central to the lateral cells according to the specific peculiarity of the plant, but it is always the *central* cell which first divides.

In the *Lycopodiaceæ* and *Equisetaceæ* the leaves also grow in length and breadth by the development of their apical and marginal cells. The Phanerogamia follow the same law. In an imperfect leaf, the cells at the border and apex are full of the homogeneous mucilage (protoplasm), while in the others it is already transformed into yellowish or greenish granular matter. Sometimes the formation of the septa may be observed in the marginal cells. In thin leaves the increase in length by the division of the *apical* cell may frequently be observed during the growth of the plant.

The fact that the leaves of Phanerogamia grow at the apex and borders and not by the base, is most easily seen in compound or much-divided leaves. As a general rule the lateral axes shoot out from the main axis in succession from below upwards; in like manner grow the tertiary axes (when present) from the secondary.

In *Astragalus* (which is figured by the author) it is shown that the uppermost leaflets are the youngest, the lowest the oldest and largest.

In *Utricularia* the growth of the leaf originally and of the divisions subsequently, may be seen to occur by continual development at the apices of the main axis and the divisions. In *Myriophyllum* however was found an exception, the upper lobes of the leaf being formed first.

The thickness of the leaf, the various inferior layers of the epidermis and the parenchyma depend on another mode of growth, which Nägeli calls, in opposition to the *peripheral cell-development, cell-development in every direction (allseitige Wachstum)*. Three forms of this occur: 1. It is either absent or merely follows at a little distance the development of the apical cell from below upward and soon ceases. In this form the development of the cells often ceases in the lower part of the leaf before it is complete at the borders. *Utricularia* is an example. 2. The development in every direction occurs simultaneously in all parts of the leaf, which completes its peripheral growth very rapidly. The growth in this form usually ceases in all parts about the same time. 3. The development in every direction begins, after the rapid completion of the peripheral growth, either only or at all events principally on the upper part of the leaf and extends downward. It ceases at the base last.

There is also sometimes an *abnormal growth in every direction*, which occurs either in particular cells or in the whole tissue, and does not appear to be subject to any laws.

The growth of leaves by the expansion of the cells is subject to various modifications.

In the Algæ the expansion does not usually begin until the growth by development is complete. It then commences in the uppermost cell and extends gradually to the base. In those branched filaments where the cells break up (*Polysiphonia*, &c.) the uppermost cell falls off first, and the process extends downward to the others in succession. There are some few exceptions to this rule, where the expansion of the cells is simultaneous, or even begins in certain other parts instead of the apex. Those Algæ however which consist of single branched cells must of course be excepted from the rule, as the expansion is the extension of one individual cell, and that proceeds from below upward.

In the Mosses and *Hepaticæ* the expansion commences, after the completion of development, at the apex and extends gradually downwards. In *Characeæ* the terminal cells expand first. In the *Lycopodiaceæ* the expansion also proceeds from the apex to the base.

In the Phanerogamia as a general rule both in simple and compound leaves, the expansion commences at the summit, but this rule is not without exception. In some leaves the expansion is tolerably simultaneous, while in others, as in *Utricularia*, it extends like the development from below upward. There does not appear to be any rule for the expansion of the petiole of compound leaves.

Drawing the conclusion as to the origin of the leaf in the higher classes from analogy, Nägeli propounds the following formulæ as the expression of his views:—

1. *The leaf originates as a simple cell.*
2. *The growth by cell-formation occurs at the apex and on the border, and proceeds, from the base, upwards and outwards.*
3. *The growth by the expansion of the cells begins, on the contrary, at the apex and extends to the base.*

Now these formulæ look remarkably definite and clear, and if we could receive them, our knowledge of these structures would be much simplified; but unfortunately, although the laws of development are simple, fundamentally, they are subject to innumerable modifications in their application, and I cannot think that Nägeli has taken all the conditions of leaves into consideration, and I believe therefore that he has generalized much too freely.

In the first place it is a question whether the fronds of the Algæ are always the analogues of leaves: if we have leaves in them, we also have leaves and stems, and probably often stems

alone ; and although he is in accordance with most authors in stating that the fronds of Algæ grow by their apices and borders, there are also exceptions here—for instance in *Laminaria digitata*, where the new frond is produced by the expansion and development of the stalk-like part of the old one. Passing by these, it is evident that the leaves of Mosses and *Hepaticæ* differ widely from those of the Phanerogamia in general in their development, though they bear considerable resemblance to such as those of *Utricularia*, &c., and many of the Monocotyledons.

The leaf of a Dicotyledon originates as a little papilla of cellular tissue : if it is a lobed leaf, these lobes appear in succession ; thus at first we see a little cone, then a three-lobed flattened papilla, next a five-lobed, and so on ; and here it is difficult to say how we shall prove, how in the five-lobed form the intermediate lobes originated—whether they are new ones, or the two original lateral lobes pushed up by two succeeding lobes—since we can only make observations on separate leaves, not *see* them grow ; but as it is clear that the papilla does grow at the base, becoming narrowed into a petiole and pushing the whole of the blade up, we have a right to assume that the leaf does in the first instance develope at its base. But then we must not generalize for the whole growth from this, since as soon as the petiole is distinctly formed, the petiole and the lamina have distinct growth ; and now the leaf in its expansion by the multiplication of its cells must grow chiefly at its borders, since the centre of the base, that is, the point of junction with the petiole, must retain its relative position, and may therefore be considered as the point of departure of all growth in the lamina ; so that as the apex and the borders are subsequently at a greater distance than at first, they must develope away from it in all directions, whether by mere marginal and apical alone or by central development also, since in the latter case the border must grow to make room for the growth in the centre. Nägeli says that the growth by expansion of the individual cells commences at the apex, but it would very often be difficult to distinguish whether this expansion at the apex depends on development of cells or actual expansion of those already formed ; he probably reasoned from analogy here in regard to the Phanerogamia. Most experiments have shown the expansion to be tolerably simultaneous throughout.

The leaves of Monocotyledons, such as those of the common bulbous plants at least, appear to develope chiefly, if not solely, at the base. In those which have petioles there must be a difference, but in such we observe the growth or actual development to continue longer in the petiole than in the blade.

The forms of leaves differing so much even in the same species, often in consequence of difference in the amount of paren-

chyma, it appears to me that the laws of growth of leaves must be looked for in the course of the development of their framework, the nerves. These are apparently organized gradually out from the stem into the nascent leaves, just as the vascular bundles into the apex of the stem, and their point of separation in the blade being fixed from the first, it is clear that all growth in the blade of the leaf must occur beyond this, and it is most natural to suppose that the nerves become organized from this centre outward as the vascular bundles were from the stem at first. Thus it would happen that Dicotyledonous leaves in general would grow at their base until they were sketched out as it were, in the bud, but as soon as the nerves were formed and the plan of the framework of the future expanded lamina laid down, the growth would be apical, marginal and interstitial. In Monocotyledonous leaves with straight veins there appears to be nothing to prevent the continued development of the base, and as we usually find the tissue in a softer and less consolidated condition there, it is probable that that part is the seat of development. These ideas are merely suggested as rational interpretations of the facts before us, but much systematic observation is required before this question can be settled.

XXIX.—On the *Ventriculidæ* of the Chalk; their classification.
By J. TOULMIN SMITH, Esq.

[Continued from p. 220.]

Genus CEPHALITES.

Character. Pouch-shaped: very constant in size and dilatation: cavity usually regular and with a single opening; sometimes winding and with more openings than one: membrane forming the wall of the cavity always deeply folded: marginal edges—and, sometimes, most prominent points—of the plaits attached to a simple apolypiferous membrane stretched across their whole breadth and forming the upper margin or head of the wall: membrane of wall polypiferous on both external and internal surfaces.

The differences between the genera *Cephalites* and *Ventriculites* are so broadly marked that, except in one or two species, it would be difficult to confound even fragments of the two. In every species of *Cephalites* the head is conspicuous and unmistakeable. This very remarkable peculiarity is alone sufficient to distinguish the genus*.

* See ante, p. 46.